formation from reptile-like progenitors, a number of simple, conical reptile-teeth came together to form each mammalian molar? Palæontology is in favour of my view; the oldest known mammals, e. g. *Triconodon* from the Upper Jura, exhibit molars of the typical structure requisite for our idea, each consisting of three similar conical tooth-segments, lying one behind the other and fused together. The admirable papers of Cope, Osborn, Schlosser, and others have shown that from the triconodont, that is the tricuspid type, the molars of all mammals may be derived.

A multitude of questions as to the specialization of the teeth within the various orders, the teeth with continuous growth, the formation of roots, &c., still remain to be answered; I shall make the attempt to do this in a detailed account of my investigations.

Jena, June 5, 1891.

XLIV.—*The Dentition of* Didelphys: *a Contribution to the Embryology of the Dentition of Marsupials* *. By W. Kükenthal †.

In the case of *Didelphys* the dental formula $\frac{5}{4}\frac{1}{1}\frac{3}{3}\frac{4}{4}$ is very generally accepted. The tooth-change is limited to one tooth, the last premolar, as was first discovered by Gervais and Flower to be the case in Marsupials. By this discovery the older view that in Marsupials the whole of the teeth are replaced with the exception of the four molars was finally overthrown. The question, however, now arose as to how the dentition of Marsupials was to be regarded, *i. e.* whether it corresponds to the milk-dentition or to the permanent series of other Mammals. While Owen was rather inclined to adopt the former view, the latter was maintained by Flower,

* Translated from a separate impression from the 'Anatomischer Anzeiger,' vi. Jahrgang (1891), nos. 23 and 24, pp. 658–666.

† In a paper which was recently published in this periodical, entitled "Einige Bemerkungen über die Säugetierbezahnung" (Anat. Anz. 1891, p. 369 [*vide suprà*, "Observations on the Dentition of Mammals," pp. 279–285]), I have already alluded to the chief result of my investigations, which formed the subject of an address delivered on the 30th of May of the present year in the Aula of our University. But, in consequence of the delay which has arisen in the setting-up of my detailed statements owing to the compositors' strike, I am now induced to give herewith a somewhat closer proof of my assertions, at least as regards the Marsupials.

thus laying the foundation of the theory that the milk-dentition has been secondarily acquired by the Mammalia, and occurs in Marsupials only in a single case (the third premolar). Although Flower's deduction was by no means generally accepted, the conception of the Marsupial dentition as belonging to the permanent or, to speak more correctly, the second series of teeth, was universally adopted. Thus it is supposed by Winge *, who otherwise in opposition to Flower regards tooth-change as an old arrangement, inherited from the lower Vertebrates, that the milk-dentition in the Marsupials has been lost, with the exception of one milk-tooth, the precursor of the third premolar. A higher grade would therefore have to be assigned to the dentition of Marsupials than to that of the majority of Mammals. "But if, contrary to all probability, it should appear that the Marsupial teeth in question have never had precursors in the course of either ontogeny or phylogeny, they would correspond to the milk-teeth in other Mammals; but they would be milk-teeth developed to such an extent that in respect of their form &c. they would have to be compared with the teeth of the second series in other Mammals."

Our knowledge of the dentition of Marsupials received a further and very material advance in consequence of Oldfield Thomas's paper †, in which the homologies of the various teeth are determined and the typical Marsupial dentition stated as consisting of 5 incisors, 1 canine, 4 premolars, and 4 molars. Reduction set in, and gave rise to the dentition of the various Marsupials; that of *Didelphys* arose in consequence of the loss of the second premolar. The third premolar, which is provided with a precursor, should therefore really be termed the fourth premolar. Thomas follows Flower in regarding the milk-dentition as having been secondarily acquired within the Mammalian class, and consistently follows out this idea. He himself points out that, besides other things, the possible discovery of the rudiments of a successor in the case of Marsupial teeth which exhibit no tooth-change would be fatal to his theory.

It was this consideration which guided me in my own investigations. If in the course of development rudiments of second

* Herluf Winge, "Om Pattedyrenes Tandskifte, især med Hensyn til Tændernes Former," Vidensk. Meddel. fra den naturh. Foren. in Kjöbenhavn, 1882, p. 52.

† Oldfield Thomas, "On the Homologies and Succession of the Teeth in the Dasyuridæ, with an Attempt to trace the History of the Evolution of Mammalian Teeth in general," Philosophical Transactions of the Royal Society (London, 1887).

teeth should be present, internal to rudiments of teeth which are subsequently cut, the proof would thus be furnished that the series of teeth which arrives at development belongs not, as was hitherto generally believed, to the second, but to the first dentition. Thus it would be shown that the milk-dentition is not to be regarded as a new and secondary acquisition within the Mammalian class.

The very fact that the third milk-premolar is cut at about the same time as the other premolars, whereupon the molars appear, commencing from the first, and that the third premolar which replaces it develops much later than the other teeth, especially than its two neighbours *, gives ground for the conjecture that the third milk-premolar belongs to the same series as the rest of the teeth which are situated in front of it. This difficulty of regarding the third milk-premolar and the other teeth as belonging to two distinct series was felt by Winge, who believed he was able to remove it by explaining that the other teeth, in spite of belonging to the second dentition, are cut simultaneously with the single milk-tooth because their precursors are wanting. Perfect clearness is naturally attainable only by means of an embryological investigation. The material at my disposal consisted in the first place of a number of lower jaws of young stages of *Didelphys*, for which I am indebted to the kindness of Prof. M. Fürbringer; my thanks are also due to Dr. Kraepelin, the Director of the Natural History Museum at Hamburg, who afterwards handed over to me for treatment a number of well-preserved young specimens of *Didelphys*, through the heads of which series of frontal sections were made. The two smallest embryos examined measured 1 centim. in length from the rump to the nape of the neck.

I select the upper jaw for the purpose of description, since the conditions in it are more distinct than those in the lower. Throughout the entire length of the upper jaw there runs a cord of epithelium, the dental fold ("Zahnleiste"), close beneath the epithelium of the cavity of the mouth; in front it is not sharply separated from the epithelium of the oral cavity, but further back, on the contrary, it lies at a greater depth. The rudiments of the enamel-organs of the five incisors appear as knobbed thickenings of the dental fold. Nothing is yet to be seen of the invagination of the enamel-organ by the dental papilla; no indication whatever of the latter is as yet presented by the rudiments of the incisors. The connective tissue surrounding the epithelial knob has

* *Vide* Thomas, *loc. cit.* p. 452.

Fig. 1.

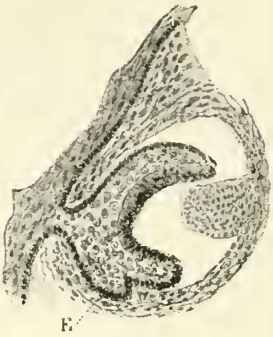


Fig. 3.

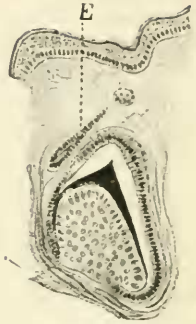


Fig. 2.

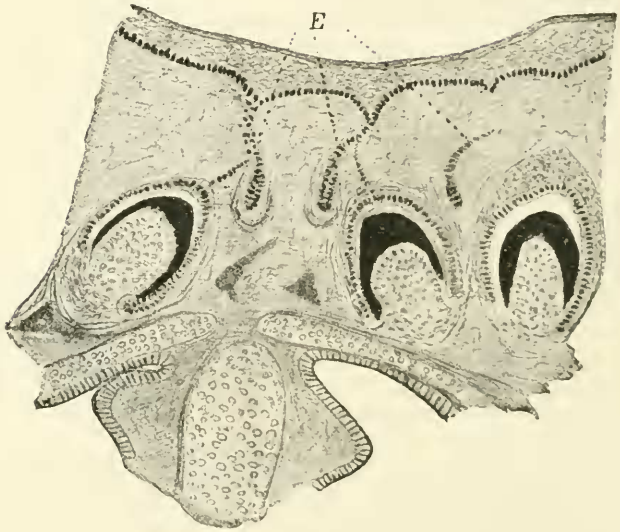


Fig. 5.

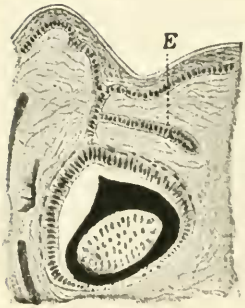


Fig. 6.

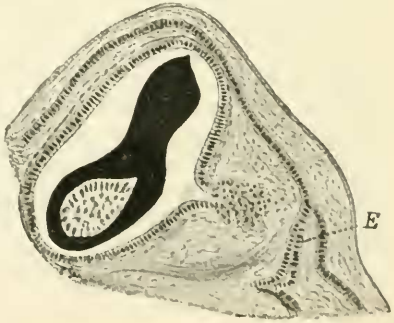


Fig. 4.

Fig. 7.

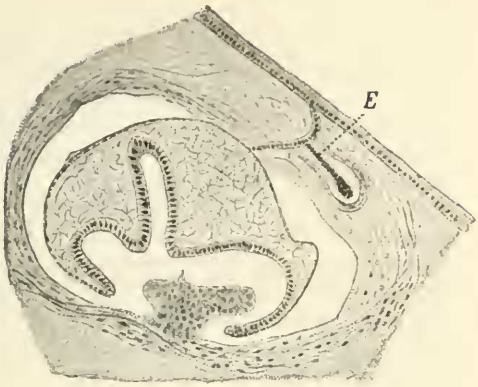
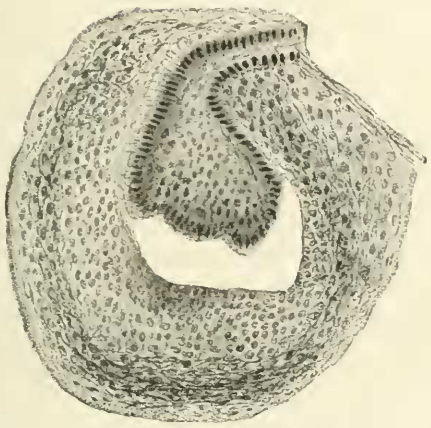


Fig. 8.



All the figures represent frontal sections through the upper jaw.
E denotes the rudiment of the enamel-organ of the second teeth.

Fig. 1.—Frontal section through the upper jaw of a young *Didelphys* measuring 1 centim. from rump to nape. The third premolar with the rudiment of the enamel-organ of the second tooth.

Fig. 2.—The first and second incisors of the upper jaw of a young *Didelphys* 3·2 centim. in length.

Fig. 3.—Third incisor of the upper jaw of a young *Didelphys* 2·5 centim. in length.

Fig. 4.—Fourth incisor of the upper jaw of a young *Didelphys* 3 centim. in length.

Fig. 5.—Fifth incisor of the upper jaw of a young *Didelphys* 3 centim. in length.

Fig. 6.—Third premolar of the upper jaw of the 3-centim. stage.

Fig. 7.—Second molar of the upper jaw of the 3·2-centim. stage.

Fig. 8.—Rudiment of the successor of the second molar of the upper jaw at the 3-centim. stage.

The figures are sketched with the help of the camera lucida. Figs. 1 and 8 with Zeiss's objective D and eyepiece no. 2, reduced by one half; figs. 2–7 with Zeiss's objective A and eyepiece no. 2, reduced by one third.

become disposed in closer concentric strands, and forms the earliest rudiment of the dental sac. The rudiment of the canine tooth is considerably larger; in the free end of the enamel-organ there is a slight indentation corresponding to the rudiment of the dental papilla, which is beginning to appear, and which is recognizable as a number of close-packed cells. The first and second premolars are scarcely distinguishable from the dental fold, while the third premolar, which comes next to them, is the most developed of all teeth (*vide* fig. 1). The enamel-organ has assumed a cap-shaped form simultaneously with the commencement of the development of the dental papilla. The inner epithelium (the enamel-membrane) exhibits the typical form of the long columnar cells, and the enamel-pulp likewise begins to develop. Internally to the wall of the jaw the enamel-organ becomes indented by an ingrowth of connective tissue and assumes a lobate form. Another series of sections from an embryo 1 centim. in length, the development of which is slightly more advanced, shows how the ingrowth of connective tissue produces further back a complete separation of the inner epithelial knob from the outer one, the original enamel-organ. The lobe which is thus constricted off can only be regarded as the earliest rudiment of the enamel-organ of the successional tooth.

Shortly after this the dental fold comes to an end, without forming any further rudiments of enamel-organs. The third premolar is therefore at this young stage far the most developed of all dental rudiments, and already exhibits the earliest indication of the enamel-organ of the successional tooth, while the rest are scarcely differentiated from the dental fold. The conditions in the lower jaw are precisely similar, though the rudiments are still less developed.

The next embryo selected for examination was considerably larger, measuring 2·5 centim. Here we find the development of the teeth greatly advanced. Commencing with the incisors, we see how a strong cap of dentine is differentiated by the odontoblasts. In the enamel-organ the enamel-pulp has become almost completely obliterated owing to the vigorous growth of the dental papilla. The internal enamel-epithelium consists of very columnar and narrow cells regularly disposed side by side; the external one forms a not altogether thin layer of flattened cells above it. The continuity of the enamel-organ with the epithelium of the cavity of the mouth is still preserved; at the same time, however, we also notice how, in the case of each of the incisors, from the tolerably broad neck a cord of epithelium projects on the inner side of

the dental rudiment and has a more or less distinctly swollen termination. The canine which follows has already attained a considerable size; nothing more than remains of an epithelial cord lying on the inner side of it is still to be seen. Its base has still not entirely disappeared from the frontal sections, when the rudiment of the first premolar is already visible above it. The latter also exhibits on the inner side a cord of epithelium with a rounded end running from the neck of the enamel-organ. It was in vain that I sought in the gap, which occurs between this premolar and the one immediately following, for a possible tooth-rudiment which had disappeared, the existence of which has been rendered so probable by Thomas's investigations: I found nothing whatever; on the contrary, the gap appeared to be relatively smaller than in the adult. The second premolar, which comes next (which is therefore the third according to Thomas), did not show the looked-for cord of epithelium, which only appeared again beside the third premolar. The dental rudiment itself is already well developed in all parts; the epithelial cord lying on the inner side of it ends in a knobbed swelling of considerable size. This concludes the investigation of the premolars; the next sections show us the conditions in the case of the molars. I was very much astonished when I saw internally to the rudiment of the first molar also, a short but distinct cord of epithelium running close beneath the epithelium of the cavity of the mouth, and still more so when the second molar also exhibited a similar epithelial cord. The conditions here were very distinct: the short and somewhat bent neck of the epithelium of the enamel-germ gave off on the inner side a lateral cord, which was of tolerable length and which thickened at the end laterally, on the inside of the dental rudiment, into a knobbed swelling of considerable size, precisely as we saw in the case of the third premolar. In connexion with this attention must also be directed to the following points:—The lateral knob of epithelium lies at a tolerable distance on the inside of the rudiment of the second molar, which has already completely developed its separate cusps; these have the same number and arrangement as in the adult animal. Moreover, the epithelial knob is absolutely lateral and not posterior in position: it has already disappeared in sections in which the rudiment of the second molar is still distinctly present. Rudiments of teeth beyond the second molar are not yet to be found.

I am now able to furnish abundant confirmation of the foregoing results, in consequence of the examination of two stages somewhat more advanced in development and measuring

3 and 3·2 centim. from rump to nape. The epithelial cords and their knobbed swellings are traceable with the utmost distinctness on the inside of the dental rudiments (*vide* figs. 2–7).

We now come to the interpretation of the facts observed. In all three larger stages we see the dental rudiments distinctly developed, and moreover an epithelial cord running close to and on the inside of them, which arises from the neck of the enamel-organ and is provided with a swollen free end. In these lateral cords of epithelium we have before us PERFECTLY TYPICAL RUDIMENTS OF THE EARLIEST STAGES OF THE ENAMEL-ORGANS OF SUCCESSIONAL TEETH, and they are indicated with special distinctness in the case of the whole of the incisors; remains of these rudiments are also seen in the case of the canine as well as in that of the first molar, and it was only in the case of the second premolar that I did not succeed in discovering them. A valuable subject for comparison is furnished by the third premolar, to which a successional tooth actually appears later on. Now the rudiment of the enamel-organ of its successional tooth agrees so entirely with that of the rudiments of the other successional teeth that there is nothing to prevent their homologization. The discovery of rudiments of successional teeth in the case of teeth other than the third premolar, which Thomas himself declared would be fatal to his hypothesis, has therefore been achieved, and moreover not in the case of one, but in that of almost all teeth. It is for the present a matter of indifference to us whether these enamel-organs of the rudiments of successional teeth undergo still further development or become rudimentary at an early period; in any case the nature of the dentition of *Didelphys*, and, as I shall immediately add, in all probability that also of the rest of the Marsupials, is settled. THE PERMANENT DENTITION OF THE MARSUPIALS BELONGS TO THE FIRST SERIES, THE MILK-DENTITION; RUDIMENTS OF THE SECOND DENTITION ARE ACTUALLY PRESENT IN AN EMBRYONIC CONDITION, BUT WITH THE EXCEPTION OF THE THIRD PREMOLAR IT DOES NOT CUT THE GUM.

A few words yet remain to be added as to the rudiments of the so-called true molars, the molars. The smallest stage, 1 centim. in length, showed as yet no trace of a rudiment either in the upper or in the lower jaw. It was only in the three subsequent larger stages that rudiments of these teeth could be detected, and here they were nearly equally far advanced in development. In the upper jaw the first and second molars were present, in the lower jaw the first, second, and third. In all cases development was already far advanced;

the separate cusps of dentine were well developed, while the spaces between the several cusps of the tooth were filled with enamel-pulp, which was surrounded by a very columnar internal and a flat external enamel-epithelium.

As has already been mentioned, a cord of epithelium running in a lateral direction is also present in the case of the first molar. The cord is, however, very little developed; it runs continuously backwards, and at the level of the dental rudiment of the second molar it comes into connexion with the enamel-organ of the latter; but simultaneously it sends off inwards a second strong cord of epithelium of considerable length, which terminates with a knobbed swelling (*vide* fig. 8). The swelling is surrounded by close-packed strands of connective tissue, arranged concentrically, and exhibits at its free end two slight indentations, while at the same time in the connective tissue, which lies beneath, the first beginnings of a papilla become visible. The structure does not lie as it might be behind the large rudiment of the second molar, but to one side of it, placed at a considerable distance towards the interior; and I can therefore not regard it otherwise than as the rudiment of a successional tooth. Thus it is demonstrated that the second molar (and naturally the first also) is in its origin in no way different from the teeth lying in front of it. THE TWO FIRST SO-CALLED MOLARS OF THE UPPER JAW BELONG TO THE FIRST DENTITION.

Shortly after the successional tooth has disappeared from the scene the second molar also disappears further backwards, and no indication appears of the rudiment of the last two molars. It is reserved for further investigations, prosecuted upon more comprehensive material, to display the earliest rudiments of these.

In the lower jaw the development of the molars has advanced further; the third molar also is already developed, somewhat smaller, it is true, than the preceding one, but still already provided with all its cusps. Here the conditions are such that, from the first molar onwards, an epithelial cord runs uninterruptedly through the posterior portion of the lower jaw, and, flattened out like a plate, passes above and laterally on the inside of the dental rudiments. It soon comes to pass that this cord has no longer any connexion with the epithelium of the cavity of the mouth, since the latter withdraws more towards the middle in consequence of the growing together of the margins of the upper and lower jaws. At each enamel-organ of the three molars a branch now passes off from this broad and very conspicuous epithelial cord, so that in each case the appearance of a dichotomic

division is presented. The enamel-organs of the molars are therefore here also in connexion with an epithelial cord, which is prolonged laterally on the inside of the dental rudiments; we have in this case also the representation of the origin of teeth of the first dentition before us, although rudiments of the second dentition are not distinctly formed. The epithelial cord terminates further back in a knobbed swelling, which is perhaps the earliest rudiment of the fourth molar.

Although the facts may yet be considerably amplified by further investigations, nevertheless I consider that I may already maintain that embryology furnishes no support for attributing the first two so-called molars of the upper jaw and the first three similar teeth of the lower jaw to another dentition than that to which are attributed the rest of the teeth which lie in front of them. There are no molars at all, but premolars. The dentition of *Didelphys* which cuts the gum and is permanent therefore belongs (with the exception of the last molars, which appear at a late stage of development) to the first series, or the milk-dentition.

XLV.—*Descriptions of new Genera and Species of* Pyralidæ *contained in the British-Museum Collection.* By W. Warren, M.A., F.E.S.

[Continued from p. 179.]

Micractis, gen. nov.

A subdivision of *Botys*. Characterized by the presence of a small raised linear dash close to the base immediately beneath the interno-median vein of the fore wing of the male. The females are always larger and generally paler than the males.

Type *M. nubilalis*, Hüb. (*Pyralis*).

Micractis sanguinealis, sp. n.

Fore wing deep yellow, more or less thickly suffused with dull red, the costa throughout deeper; lines themselves reddish; first curved outwardly, preceded by a yellowish space, the basal area up to it suffusedly reddish; central space between the two lines thickly suffused with red, the two stigmata deeper; second line, slightly serrated, forms a distinct